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Influence of surrounding vegetation on woodpecker nest tree selection in oak forests of the Upper Midwest, USA

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Abstract

This study examined the influence of forest context on woodpecker nest tree selection, which has implications for forest managers leaving trees during timber harvest for cavity nesting birds. We surveyed habitat variables in 11.3 m radius subplots centered on 165 active woodpecker nest trees and 144 randomly selected points in oak forests of southeastern Minnesota and western Wisconsin in 1997–1998. Forward stepwise sequential F-tests indicated that the number of potential nest trees and basal area (BA) of dead elms were the most important variables in distinguishing nest sites and random sites. Discriminant function analysis correctly classified 71% of the observations. However, a comparison of nest sites only to those random sites containing a tree likely suitable for nesting showed no differences. This suggests that nest tree has a greater influence in nest site selection than does surrounding vegetation. Yellow-bellied sapsucker nest trees were surrounded by a significantly higher BA of trembling aspen (*Populus tremuloides*) and density of mast-producing trees than the nest trees of the downy, hairy, red-bellied, red-headed, and pileated woodpeckers, and the northern flicker. However, we found no interspecific differences among downy, hairy, red-bellied, and red-headed woodpeckers. This study is significant because it indicates forest management for cavity nesting birds should focus on providing suitable nest trees within the larger forest context; vegetation immediately surrounding nest trees may have minimal influence on woodpecker nest tree selection.

Keywords: Woodpeckers; Cavity nesting birds; Dead standing trees; Nest trees

1. Introduction

Woodpeckers are important members of forest communities. As primary cavity nesting birds, woodpeckers excavate holes in trees for nesting and roosting. Secondary cavity nesting wildlife later uses these holes. For example, 23 species of birds in Minnesota use old woodpecker nest holes for nesting (Green, 1995). Mammals (e.g. squirrels and bats) also use tree cavities as dens or cover. Woodpecker nest hole excavation requires that trees contain some heartwood decay (Kilham, 1971; Conner et al., 1976). Thus, many woodpeckers are dependent on dead and dying trees for nesting.

Through eliminating old or dead trees, intensive forest management may lower populations of cavity nesting birds. A decline in several species of cavity nesting birds in our study area was predicted based on intensity of timber harvest in the 1994 Generic Environmental Impact Statement on Timber Harvesting and Forest Management in Minnesota. Many studies have shown a relationship between density of dead trees and abundance of cavity nesting birds (Dickson and

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Conner, 1983; Scott and Oldemeyer, 1983; Zarnowitz, 1983; Raphael and White, 1984; Stribling et al., 1990).

Careful management during timber harvest can reduce impacts on cavity nesting birds. Scott and Oldemeyer (1983) found that densities of cavity nesting birds decreased by 53% when conifer snags were removed during harvest of ponderosa pine (*Pinus ponderosa*) forests in Arizona, but on an adjacent plot where snags were left standing during timber harvest, they found that densities of cavity nesting birds increased by 25%.

Research on cavity nesting birds is needed to develop forest management guidelines that balance needs of wildlife with timber production. There have been numerous studies on the characteristics of woodpecker nest trees (Kilham, 1971; Reller, 1972; McClelland and Frissell, 1975; Conner et al., 1976; Bull and Meslow, 1977; Scott, 1978; Mannan et al., 1980; Stauffer and Best, 1982; Scott and Oldemeyer, 1983; Welsch and Howard, 1983; Raphael and White, 1984; Zarnowitz and Manuwal, 1985; Sedgwick and Knopf, 1986; Swallow et al., 1986; Keisker, 1987; Runde and Capen, 1987; Li and Martin, 1991; Shreiber and deCalesta, 1992). Research on habitat surrounding woodpecker nest trees, however, is more limited (Conner et al., 1975; Conner and Adkisson, 1977; Brawn et al., 1984; Raphael and White, 1984; Petit et al., 1985; Swallow et al., 1986; Sedgwick and Knopf, 1990; Li and Martin, 1991).

We are unaware of any study specifically examining characteristics of vegetation surrounding active nests of cavity nesting birds in the Upper Midwest. However, there are a few studies from the Upper Midwest that offer insight into importance of forest context for cavity nesting birds. In a study of relationships of birds to habitat characteristics in logged areas of northern Minnesota, Niemi and Hanoski (1984) reported little evidence to support any relationship between number of dead trees and abundance of most species of cavity nesting birds. Howe et al. (1995) found six of the nine species that showed no significant relationships with overall forest characteristics were cavity nesting birds. They speculated overall forest characteristics were less important to species with specific nest tree requirements. However, Schulte and Niemi (1998) found the house wren (*Troglodytes aedon*) and eastern bluebird (*Sialia sialis*) were associated with higher densities of dead trees and more variation in dead trees in early-successional forests of northern Minnesota.

Without knowledge of specific habitat requirements of cavity nesting birds, development of timber management guidelines to favor these species is difficult. For example, many national forest plans of eastern USA address number and distribution of trees of various size classes that should be left during harvest, but they do not address broader habitat requirements of cavity nesting birds (US Forest Service, 1981, 1986a,b, 1987a,b, 1988, 1995). Additionally, it is unclear whether one set of guidelines can address the needs of all woodpecker species in each forest. If habitat requirements vary widely among species, guidelines will need to be broad enough to address the breeding requirements of all species.

The purpose of this study was to obtain information on habitat surrounding woodpecker nest trees in oak forests of the Upper Midwest to determine if surrounding vegetation influences nest tree selection. Many previous studies concluded that vegetation surrounding woodpecker nest trees influences nest tree selection (Raphael and White, 1984; Conner et al., 1975; Swallow et al., 1986), but none separated influence of nest tree from influence of surrounding vegetation. The influence of surrounding vegetation may have ramifications for the distribution of trees left during timber harvest for cavity nesting birds. It can also guide whether management should be focused on nest trees or on broader habitat requirements. To address the question of whether general guidelines are suitable for all species, we also examined if characteristics of surrounding vegetation differed among woodpecker species.

We located active woodpecker nests and surveyed vegetation of nest sites and random sites. We tested the following null hypotheses: (1) there is no difference in vegetation between woodpecker nest sites and random sites; (2) there is no difference in vegetation between woodpecker nest sites and random sites that include a tree likely suitable for nesting; and (3) there is no difference in vegetation among nest sites of woodpecker species.

2. Study area and methods

2.1. Study area

The study area was composed of Houston and Filmore counties in southeastern Minnesota, USA

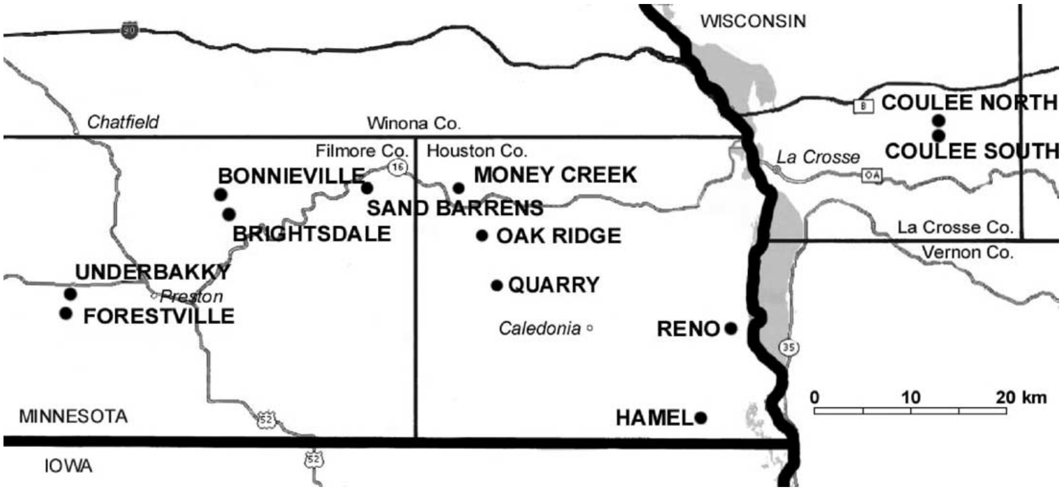

Fig. 1. Map of Houston and Filmore counties of Minnesota and La Crosse county of Wisconsin showing locations of 12 study plots in oak forests of the Upper Midwest, USA, 1997–1998.

and La Crosse county in western Wisconsin, USA (43°N, 91°W; Fig. 1). The pre-settlement vegetation was oak woodland and brushland and maple-basswood forest (Marschner, 1974). The current landscape is highly fragmented, consisting primarily of oak forest patches surrounded by agricultural lands.

We selected plots from available state-owned forests that were accessible by road and received infrequent public use. Because plots were not randomly selected, forest characteristics may not be entirely representative of the Upper Midwest. The level of representation is improved, however, by the fact that plots were widely scattered, with about 90 km between westernmost and easternmost plots. Topographic maps of study areas, location descriptions based on US Public-Land Survey System, and additional details on methods are in Adkins Giese (1999).

All plots were in mature forest, aged 80–120 years, with a component of dead and dying trees. The canopies were dominated by oaks (*Quercus rubra*, *Q. alba*, *Q. bicolor*) and hickories (*Carya ovata*, *C. cordiformis*), but also included elm (*Ulmus americana*, *U. rubra*), basswood (*Tilia americana*), aspen (*Populus tremuloides*, *P. grandidentata*), other hardwoods, and some white pine (*Pinus strobus*). Young individuals of these canopy tree species, hazel (*Corylus* spp.), gooseberry (*Ribes* spp.), and raspberry (*Rubus* spp.) made up the woody understory. Breeding bird surveys during 1997 indicated that the plots had 56 bird species, including 13 cavity nesting species (M. Friberg, pers. comm.).

Plots were 28–40 ha (mean = 36 ha). We marked the plots with flagging tape, forming grids spaced at 50 or 100 m intervals. Grids were used to locate woodpecker activity on field maps, to mark nest sites, and to locate the randomly selected sampling subplots.

2.2. Nest searching

In 1997, we searched for woodpecker nests 6 May through 23 June, and in 1998, from 20 April to 22 June. After formal nest searching ended, we opportunistically found additional active nests during vegetation surveys. We searched for active nests of all locally breeding woodpeckers on the plots: downy (*Picoides pubescens*), hairy (*Picoides villosus*), red-bellied (*Melanerpes carolinus*), red-headed (*Melanerpes erythrocephalus*), and pileated (*Dryocopus pileatus*) woodpeckers, yellow-bellied sapsuckers, and northern flickers (*Colaptes auratus*).

Searches began at dawn and involved following woodpecker vocalizations, drumming, and flight paths. We located additional nests by systematically walking the plots and examining trees with indications of possible use, such as cavities and fresh chips at the base. Nests of the red-headed woodpecker were found along roadsides, as well as on the plots.

We confirmed nests as active if we observed any of the following: (1) adult completely entering nest hole and remaining in cavity for over 10 min; (2) adult flushed from nest hole; (3) adult feeding young; and (4) young calling from cavity. Because of difficulty locating red-headed woodpecker nests, we relaxed our criteria; an adult repeatedly entering the nest cavity but not remaining inside was considered sufficient evidence of activity. We found 165 active woodpecker nest trees.

2.3. Vegetation surveys

We designed this study to compare nest sites to random forest sites to determine if woodpeckers choose among habitats when selecting nest sites. However, in this comparison, the influence of the nest tree could not be separated from the influence of surrounding vegetation. To minimize the influence of the nest tree, we also compared nest sites to random sites containing a tree likely suitable for nesting.

We surveyed vegetation at woodpecker nest sites and at random sites during the summers of 1997 and 1998. Vegetation surveys of random sites began after formal nest searching ended, while surveys of nest sites began shortly after the nestlings fledged. Surveys were completed within one month to minimize the impact of changing forest conditions with time. Survey methods were modified after Martin and Conway (1994).

Aspects of habitat were measured in 11.3 m radius circular subplots centered on active woodpecker nest trees and randomly located points. Random points were located at 15 m from a randomly selected grid-point in a randomly selected azimuth. Nine random subplots were surveyed on each of the eight plots during each field season, for a total of 144 random sites, representing 1% of the total study area.

Within the subplots, data to describe the canopy, forest floor, and trees were recorded. To characterize the canopy, we recorded canopy height, total canopy cover, and high canopy cover. To describe the forest floor, we recorded slope, shrub cover, and downed wood cover. Measurements of canopy, shrub, and downed wood cover were taken in each of the four principle directions, 5 m from plot center. To obtain data on the density and basal area (BA) of various tree species, we recorded size, status, and species of all trees within the subplots.

Potential nest trees were defined as trees unused for nesting, within the height and diameter requirements of cavity nesting birds, with at least two indicators of heartwood decay (Conner, 1978). In accordance with minimum nest height and tree diameter requirements for woodpeckers, potential nest trees were >15.2 cm diameter at breast height (DBH) and >1.8 m tall (Thomas et al., 1979). Size and condition of all potential nest trees within subplots were recorded, as these trees are likely important to woodpeckers for nesting, roosting, and foraging. Potential nest tree measurements included: species, DBH, height, status, top condition, limb condition, percent live wood and percent bark cover in quartile classes, and presence of decay indicators including old cavities, tree scars, branch stubs, fungal conks, and significant dead portions.

Random sites containing a tree likely suitable for nesting were defined as suitable sites. Trees suitable for nesting were defined as elm or trembling aspen trees with more than two decay indicators or potential nest trees with old cavities. We used these tree characteristics as defining criteria because they accounted for a significant difference between active woodpecker nest trees and adjacent unused potential nest trees in this study area (Adkins Giese, 2002). Twenty-three random subplots contained at least one suitable tree and were used for comparison to nest sites on the plots.

2.4. Data analysis

We compared nest sites to random sites and, to minimize the influence of the nest tree, compared nest sites to suitable sites. Both comparisons were used to evaluate influence of surrounding vegetation in woodpecker nest tree selection. Wilk's λ was used in these comparisons to test for multivariate differences (Johnson and Wichern, 1992). If a significant difference was found ($\alpha = 0.05$), we used Bonferronized univariate F-tests to see which variables accounted for the differences (Kuehl, 1994). Forward stepwise sequential F-tests were used to select variables for discriminant function analysis. We started by selecting the variable with the most significant univariate F, and then included the variable with the largest univariate F when the first variable was used as a covariate. The selection process continued until no variable had a high enough sequential F to be included ($\alpha = 0.15$). We Bonferronized all F-statistics at each stage, using the number of "out" variables as the number of tests. The discriminant function analysis combined the selected habitat variables into the one function that most effectively separated the groups (Johnson and Wichern, 1992). The number of correctly classified observations indicated the strength of the separation.

To determine if any similarities or differences in habitat existed among woodpecker species, we did two additional analyses. Upon initial examination of the habitat data, it was clear that the habitat of the yellow-bellied sapsucker differed greatly from the habitat of other species of woodpeckers. While one multivariate comparison among all woodpecker species may seem appropriate, this approach would fail to detect subtle differences in habitat among the downy, hairy, red-bellied, and red-headed woodpeckers. Consequently, we separated the analysis among the woodpecker species into two separate multivariate analyses. We compared the yellow-bellied sapsucker to the other woodpeckers to determine which habitat variables were most important in separating the yellow-bellied sapsucker from the other woodpecker species. Then, we compared habitat among the downy, hairy, red-bellied, and red-headed woodpeckers. We excluded pileated woodpeckers and northern flickers from this analysis because of low sample size.

The 24 habitat variables used included: percent total canopy cover, percent high canopy cover, canopy height, slope, genus-level richness, genus-level diversity, percent shrub cover, percent downed wood cover, and number and BA of total trees, trembling aspen, dead trees, dead or partly dead (PD) trees, dead or PD trees >38 cm DBH, dead elms, potential nest trees, and mast-producing trees per hectare. Mast-producing trees included all living oak trees, hickory trees, and black walnut (*Juglans niger*); we included this habitat variable because red-headed and red-bellied woodpeckers rely on mast as a food source. We transformed data as necessary to meet assumptions of normality and equal variance (Box and Cox, 1964). Macanova was used for all computations (Oehlert and Bingham, 1998).

3. Results

3.1. A comparison of nest sites and random sites

We found significant differences between nest sites and random sites when all habitat variables were considered simultaneously (Table 1; Wilk's $\lambda = 104$, $P < 0.001$). When each variable was considered separately using F-tests, 10 of the 24 habitat variables showed significant differences (Table 2). Density of potential nest trees and the BA of dead elms were selected for discriminant function analysis ($P < 0.15$). Separation of habitat based on the discriminant function was also significant ($F = 69$; d.f. $= 2286$; $P < 0.001$). When we used the discriminant function to classify each observation as either a nest site or random site, 71% of observations were classified correctly.

3.2. A comparison of nest sites and suitable sites

To minimize influence of the nest tree, we compared nest sites to random sites containing a tree suitable for nesting. We were unable to detect any differences between nest sites and suitable sites using multivariate or univariate tests (Wilk's $\lambda = 14$, $P = 0.95$). Forward stepwise variable selection did not select any variables for discriminant function analysis ($P > 0.15$), which indicated similarity between nest sites and suitable sites.

3.3. A comparison of yellow-bellied sapsucker to the other woodpeckers

In a comparison between yellow-bellied sapsucker and all other woodpecker species nest sites, we detected a strong difference in habitat when we considered all habitat variables simultaneously (Wilk's $\lambda = 73$, $P < 0.001$). When we considered each habitat variable separately using F-tests, six of the 24 habitat variables showed significant difference (Table 3). BA of trembling aspen and density of mast-producing trees were selected for discriminant function analysis. The separation of habitat based on the discriminant function was also significant ($F = 39$; d.f. $= 2162$; $P < 0.001$). In using the discriminant function to classify each observation as either a yellow-bellied sapsucker nest site or a nest site of the other woodpecker species, 82% of observations were classified correctly.

3.4. A comparison among the other woodpecker species

Habitat was marginally significantly different among downy, hairy, red-bellied, and red-headed

Table 1
Mean values and standard errors for vegetation characteristics of nest sites and randomly located sites in oak forests of the Upper Midwest, USA, 1997–1998

	DOWO[a] (44)[b]		HAWO[c] (22)[b]		RBWO[d] (29)[b]		RHWO[e] (20)[b]		PIWO[f] (4)[b]		NOFL[g] (4)[b]		YBSA[h] (42)[b]		OTHER THAN YBSA[i] (123)[b]		All[j] (165)[b]		Random (144)[b]		Suitable (23)[b]	
	x	S.E.	*x*	S.E.	*x*	S.E.	*x*	S.E.	*x*	S.E.	*x*	S.E.	*x*	S.E.	*x*	S.E.	*x*	S.E.	*x*	S.E.	*x*	S.E.
Total trees/ha	583	31	584	47	601	34	514	75	786	247	231	33	743	21	571	22	614	19	613	16	721	32
Trembling aspen/ha	24	8	35	17	14	5	24	15	94	94	0	0	131	17	25	6	52	7	33	9	78	22
Dead trees/ha	103	11	93	12	84	12	123	15	106	41	62	24	110	8	99	6	102	5	73	5	111	16
Dead or PD trees/ha	112	12	105	12	90	12	126	15	112	47	62	24	120	9	106	6	110	5	83	5	120	16
Dead or PD >38 cm DBH/ha	16	3	18	5	21	4	32	6	19	6	19	6	8	3	21	2	18	2	10	1	11	5
Dead elms/ha	44	9	40	10	31	10	61	14	44	21	62	24	20	5	43	5	37	4	12	2	17	6
Mast-producing trees/ha	199	21	202	31	203	28	204	45	237	212	19	12	312	23	197	15	226	13	270	14	282	40
Potential nest trees/ha	4	0.3	4	0.4	3	0.3	5	0.5	3	1.2	3	0.9	6	0.5	4	0.2	5	0.2	3	0.2	5	0.6
Percentage total canopy cover	95	1	91	4	94	3	68	8	93	5	69	9	98	0.3	89	2	91	2	97	0.3	97	0.5
Percentage high canopy cover	94	2	90	4	93	3	67	8	92	4	65	13	96	1	87	2	89	2	95	0.3	96	0.7
Canopy height (m)	20	0.5	18	0.6	20	0.8	20	1.0	19	2.9	19	2.1	20	0.4	19	0.3	19	0.3	21	0.3	20	1.0
Plot slope (°)	11	1.0	12	1.6	11	1.7	7	2.0	4	2.3	8	4.4	9	1.1	10	0.7	10	0.6	13	0.6	10	1.5
BA of trees (m^2/ha)	32	1.6	29	1.8	34	2.2	35	3.7	43	4.6	31	4.7	38	1.4	33	1.0	34	0.9	30	0.8	33	2.1
BA trembling aspen (m^2/ha)	1.8	0.7	2.0	0.9	1.2	0.5	1.5	1.0	4.4	4.4	0.0	0.0	9.3	1.2	1.7	0.4	3.6	0.5	1.6	0.4	4.5	1.5
BA dead trees (m^2/ha)	5.9	0.7	6.2	1.2	7.9	1.6	11.2	1.2	14.3	7.7	12.8	6.1	4.8	0.6	7.8	0.6	7.0	0.5	3.2	0.3	5.4	1.0
BA dead or PD trees (m^2/ha)	6.5	0.8	7.3	1.3	8.5	1.5	11.3	1.2	14.3	7.7	12.8	6.1	5.3	0.7	8.3	0.6	7.6	0.5	4.1	0.3	5.9	1.1
BA dead or PD >38 cm DBH	2.9	0.6	4.2	1.2	5.9	1.7	7.0	1.4	12.0	8.4	11.9	6.1	1.4	0.5	5.1	0.6	4.1	0.5	1.9	0.3	2.0	1.1
BA dead elms (m^2/ha)	3.2	0.7	3.3	0.9	4.4	1.7	6.6	1.4	12.2	8.7	12.8	6.1	1.1	0.4	4.7	0.7	3.7	0.5	0.4	0.1	0.9	0.3
BA mast trees (m^2/ha)	15	1.7	12	1.7	16	2.2	14	3.1	6	6.1	5	4.0	19	1.7	14	1.0	15	0.9	19	0.9	17	2.0
BA potential nest trees (m^2/ha)	10	0.9	10	1.6	12	1.5	16	2.3	14	6.2	23	6.2	12	1.0	12	0.8	12	0.6	7	0.6	9	1.4
Genus-level richness	5	0.3	5	0.4	5	0.3	5	0.6	4	0.3	3	0.5	6	0.2	5	0.2	5	0.1	5	0.1	6	0.3
Genus-level diversity	1.8	0.1	2.0	0.1	2.0	0.1	1.6	0.2	1.3	0.2	1.4	0.2	2.1	0.1	1.8	0.1	1.9	0.0	2	0.0	2.0	0.1
Percentage shrub cover	25	3	27	5	31	4	14	2	18	7	22	12	27	3	24	2	25	2	27	1	31	4
Percentage downed wood	6.5	1.2	4.9	1.2	4.6	1.0	6.0	1.3	7.5	3.3	2.8	2.8	5.7	0.7	5.6	0.6	5.6	0.5	4	0.4	4.4	1.1

[a] Downy woodpecker (*Picoides pubescens*).
[b] Sample size.
[c] Hairy woodpecker (*P. villosus*).
[d] Red-bellied woodpecker (*Melanerpes carolinus*).
[e] Red-headed woodpecker (*M. erythrocephalus*).
[f] Pileated woodpecker (*Drycopus pileatus*).
[g] Northern flicker (*Colaptes auratus*).
[h] Yellow-bellied sapsucker (*Sphyrapicus varius*).
[i] Downy, hairy, red-bellied, red-headed, and pileated woodpeckers, and the northern flicker.
[j] Includes nests of all woodpecker species.

Table 2
Mean values, F-statistics, and Bonferronized P-values for variables that differed significantly between nest sites and randomly located sites in oak forests of the Upper Midwest, USA, 1997–1998[a]

	Nest Sites[b]		Random Sites[b]		F-statistics	Bonferronized P-values
	S.E.	Mean	Mean	S.E.		
Potential nest trees/ha[c]	0.2	5	3	0.2	41.9	<0.001
Basal area (BA) of dead elms (m^2/ha)[c]	0.5	4	0	0.1	32.7	<0.001
Basal area dead trees (m^2/ha)	0.5	7	3	0.3	23.0	<0.001
BA potential nest trees (m^2/ha)	0.6	11.8	7.3	0.6	22.2	<0.001
Dead elms/ha	4.0	37	12	1.9	21.0	<0.001
BA dead or partly dead trees (m^2/ha)	0.5	8	4	0.3	16.6	0.001
BA trembling aspen (m^2/ha)	0.5	4	2	0.4	15.4	0.003
BA trees (m^2/ha)	1	34	30	1	9.9	0.043
Dead trees/ha	5	102	73	5	9.8	0.045
Canopy height (m)	0.3	19	21	0.3	9.7	0.048
% correctly classified	64		83			

[a] Percentages of points correctly classified using the discrimination function are also included.
[b] Means and standard errors are based on untransformed data.
[c] Selected by stepwise analysis and used in classification.

Table 3
Mean values, F-statistics, and Bonferronized P-values for variables that differed significantly between yellow-bellied sapsuckers and six other species of woodpecker in oak forests of the Upper Midwest, USA, 1997–1998[a]

	Yellow-bellied sapsucker[b]		Other woodpeckers[b]		F-statistics	Bonferronized P-values
	S.E.	Mean	Mean	S.E.		
BA of trembling aspen (m^2/ha)[c]	1.2	9	2	0.4	44.6	<0.001
Trembling aspen/ha	17	131	25	6	38.9	<0.001
Potential nest trees/ha	0.5	6	4	0.2	24.0	<0.001
Genus-level richness	0.2	6.4	5.0	0.2	13.6	0.007
BA dead or PD >38 cm DBH (m^2/ha)	0.5	1.1	4.7	0.6	12.1	0.015
Mast-producing trees/ha[c]	23	312	197	15	11.9	0.017
Percentage correctly classified	74		85			

[a] Percentages of points corrected classified using the discriminant function are also included.
[b] Means and standard errors are based on untransformed data.
[c] Selected by stepwise analysis and used in classification.

woodpeckers (Wilk's $\lambda = 93$, $P = 0.047$). No significant differences were found when each habitat variable was considered separately using Bonferronized F-tests. No variables had a strong enough effect in distinguishing the groups to be selected for discriminant function analysis ($P > 0.15$).

4. Discussion

4.1. A comparison of nest sites and unused sites

Density of potential nest trees and BA of dead elms were the most important variables distinguishing between nest sites and random sites, and dead elms were very important nest trees for woodpeckers in this study area (Adkins Giese, 2002). This may indicate that woodpeckers are choosing nest trees surrounded by other trees probably suitable for nesting. Li and Martin (1991) suggested woodpeckers might choose nest trees surrounded by potential nest trees to reduce predator efficiency because predators would be forced to search more sites. Trees surrounding nest trees may also be important habitat for woodpecker prey. We casually observed woodpeckers foraging on dead elms and other trees with decay indicators.

Other investigators also reported differences between woodpecker nest sites and random sites (Raphael and White, 1984; Conner and Adkisson, 1977). However, it was unclear whether the differences they reported actually influenced nest tree selection. Even though a significant difference in habitat between nest sites and random sites was found, it cannot be assumed that vegetation surrounding the nest tree actually influenced nest tree selection. Characteristics of adjacent trees are not independent. Disease can spread among nearby trees, a strong wind may break branches of a group of trees, or a clump of trees may grow larger because of ideal growing conditions at their location. We observed clumps of dead and dying trees in the study area. Land et al. (1989) found that snags are often found in clumps in Florida slash pine plantations. Therefore, it is difficult to separate the influence of the nest tree from the influence of surrounding trees in nest site selection.

Other investigators compared nest sites to random sites centered on snags (Li and Martin, 1991; Swallow et al., 1986; Brawn et al., 1984). In this approach, nest tree influence is less than if random sites were representative of available habitat. However, the influence of surrounding habitat is still confounded by the influence of the nest tree. For example, snags chosen for random site centers may be smaller on average than snags chosen for nesting and likewise be surrounded by smaller snags. This connection would give the questionable result that the larger snags surrounding the nest trees influenced selection.

An ideal research design would compare nest sites and random sites centered on nearly identical nest trees. Petit et al. (1985) achieved this design in a study done in oak–hickory forests of Ohio. They compared habitat surrounding used and unused randomly located polystyrene artificial snags. They found lower percentage canopy cover, fewer small trees, and fewer total trees surrounded artificial snags selected for nesting.

Within the constraints of our research design, we developed a comparison that did not confound influence of the nest tree with influence of surrounding vegetation. We compared nest sites to suitable sites, which were random sites that contained a tree likely suitable for nesting. Our definition of suitable sites may not fully reflect woodpecker preference, but given that each suitable site contained an unused tree likely suitable for nesting, we conclude that any difference in habitat between nest sites and suitable sites contributed to the difference in selection. The crucial result was that no habitat variables could distinguish nest sites and suitable sites. This is important because it suggests that surrounding vegetation may have minimal influence on nest tree selection. However, differences in surrounding vegetation may exist for characteristics that we did not measure, and it is possible that selection is so variable that we did not have adequate statistical power to detect differences in surrounding vegetation. Our results are supported by the findings of Howe et al. (1995), who found no significant habitat associations for downy, hairy, and pileated woodpeckers and the northern flicker in Nicolet National Forest, western Wisconsin, USA. The investigators asserted that these birds select specific nest trees so overall forest characteristics may be less important.

4.2. A comparison among woodpecker species

We were also interested in whether characteristics of habitat surrounding nest trees differed among woodpecker species. In this study, BA of trembling aspen was an important variable separating habitat of the yellow-bellied sapsucker from all other woodpecker species combined. The habitat association between sapsuckers and aspens has been well documented (Evans and Conner, 1979; Thomas et al., 1979; Westworth and Telfer, 1993). Many studies have shown that yellow-bellied sapsuckers use aspen trees for nesting (Kilham, 1971; McClelland, 1977; Scott et al., 1980; Runde and Capen, 1987; Adkins Giese, 2002). Yellow-bellied sapsuckers are weak excavators (Jackman, 1974) and likely find the extensive heartwood decay of mature aspen suitable for excavation (Adkins Giese, 2002). Given that aspens grow in clumps, the high BA of aspens surrounding the nest trees is likely a result of sapsuckers selecting aspens for nest trees. It is unclear why density of mast-producing trees is an important variable separating nest sites of yellow-bellied sapsuckers from the other woodpeckers. In our study, yellow-bellied sapsuckers rarely used mast-producing trees for nesting (Adkins Giese, 2002). Any correlation with mast-producing trees is likely an artifact of other unmeasured aspects of habitat.

Habitat surrounding nest trees was quite similar for downy, hairy, red-bellied, and red-headed woodpeckers in our study. Extensive overlap in habitat requirements for hairy and downy woodpeckers has been previously observed (Conner and Adkisson, 1977), but our finding that habitat of red-headed woodpeckers could not be distinguished from habitat of downy, hairy, or red-bellied woodpeckers is unusual. Conner and Adkisson (1977) found no overlap in BA, density of stems, and canopy height between downy or hairy woodpeckers and red-headed woodpeckers in oak–hickory forests. Other researchers have also documented the propensity of red-headed woodpeckers to nest in open areas (Scott et al., 1977; Robbins et al., 1983). In our study, more than half of red-headed woodpecker nests were found in closed canopy forests. It is possible that our relaxed criteria for determining active red-headed woodpecker nests overestimated nests within closed canopy forests. However, it is probable that continued removal of snags in agricultural areas, blow-downs, and competition from European starlings (*Sturnus vulgaris*) (Harrison, 1975; Adkins Giese, pers. obs.) have forced red-headed woodpeckers into closed canopy forests. Nesting in closed canopy forests may force red-headed woodpeckers to compete for nest trees with red-bellied woodpeckers and southern flying squirrels (*Glaucomys volans*). We observed aggressive interactions between red-headed and red-bellied woodpeckers at nest trees. Additionally, several red-headed woodpecker nests were usurped by southern flying squirrels during the breeding season.

4.3. Management implications

We found a difference in habitat between nest sites and random sites, but this difference may be explained by the influence of the nest tree. Woodpeckers may select nest trees with certain characteristics independent of the surrounding vegetation, but because trees with these characteristics tend to occur in patches, it appears that surrounding vegetation influenced nest tree selection. The important result of this study is that no habitat variables could distinguish between nest sites and random sites that contained a tree suitable for nesting. This suggests that management for cavity nesting birds should be focused on nest trees rather than broader habitat requirements. Several investigators have argued that vegetation surrounding woodpecker nest trees influences nest tree selection (Raphael and White, 1984; Conner et al., 1975; Swallow et al., 1986), but none separated influence of nest tree from influence of surrounding vegetation.

Whether or not surrounding vegetation actually influenced nest tree selection, woodpeckers clearly chose nest trees in patches containing high densities of potential nest trees and high BA of dead elms. While we did not design our study to determine if trees left during harvest should be scattered or clumped, the fact that nest trees were surrounded by snags suggests that leaving clumps of snags for cavity nesting birds during harvest would likely be beneficial. However, the literature includes disagreement as to whether trees left during harvest should be scattered or clumped. Some investigators recommend that individual trees be evenly distributed across the harvest area because woodpecker territoriality limits the use within each clump (Evans and Conner, 1979). Ryan (1995) found that birds used isolated snags much more than clumped snags in northern Wisconsin clearcuts. Additionally, secondary cavity nesting birds like American Kestrels (*Falco spaverius*), eastern bluebirds, and tree swallows (*Tachycineta bicolor*) prefer tree cavities in open areas (Green, 1995). However, other investigators argue that a clumped distribution is best (McClelland, 1977; Raphael and White, 1984). Lawrence (1966) found no interspecific territorial behavior when woodpeckers nested in close proximity in northern hardwoods of Ontario. Raphael and White (1984) suggested that clumping trees left during harvest increases foraging efficiency by reducing intertree flight time, and Gibbons (1994) argued that trees immediately surrounded by other living trees persist longer. Clusters also provide trees for future nesting and roosting (Bull and Meslow, 1977). From a timber management perspective, a clumped distribution may be a practical necessity. A clumped distribution can reduce the spread of genetically inferior trees from snags and reduce widespread retardation of growth around reserve trees (Styskel, 1983). Modeling studies are needed to weigh the effects of increased snag longevity in clumps and increased woodpecker use of isolated trees.

Management for yellow-bellied sapsuckers is less ambiguous. This species chooses nest trees within clumps of mature aspens. Because aspens are highly susceptible to blow-downs and yellow-bellied sap-

Table 4
Snag management in USDA Forest Service national forests with a significant oak component in Eastern Region USA

National forest (location, year plan published)	Preferred location or distribution
Mark Twain (Missouri, US Forest Service, 1986a)	Not specified
Shawnee (Illinois, US Forest Service, 1986b)	Clumps (1/3 to 1/5 acre per 5 acres) with many specifics for preferred clump locations
Hoosier (Indiana, US Forest Service, 1987a)	In hollows and along stand borders and retain all dead and dying near streams
Wayne (Ohio, US Forest Service, 1987b)	Not specified
Monogahela (West Virginia, US Forest Service, 1995)	Must not affect scenic attributes or the stand or public safety
Allegheny (Pennsylvania, US Forest Service, 1988)	Leave snags and clumps of trees surrounding den trees primarily in hollows and along stand borders

suckers tolerated nesting in close proximity, we suggest forest managers leave clumps of mature aspens for yellow-bellied sapsuckers. Aspens are popular nesting substrates for other woodpecker species as well (Li and Martin, 1991; Adkins Giese, 2002), so clumps of mature aspen are likely to be widely used. It is important that these clumps are not harvested before they have matured to the point where they become suitable for woodpeckers. Old growth conditions may take >100 years in some aspen forests (Winternitz and Cahn, 1983), but are considerably shorter in others (Green, 1995).

Habitat did not differ among downy, hairy, red-bellied, or red-headed woodpeckers. This suggests that general habitat management guidelines would suit the needs of these woodpecker species. During harvest, managers should leave clumps of dead and dying trees, especially dead elms, for these woodpeckers. In our study, the most nests were found in the plot with the highest density of dead trees. While more research is needed to determine the best distribution of trees left during harvest, snags are clearly an important component of forest structure and should be retained during harvest.

Snag and cavity tree management guidelines for national forests in eastern USA offer few recommendations in terms of habitat surrounding cavity trees (US Forest Service, 1981, 1986a,b, 1987a,b, 1988, 1995). Instead, most guidelines focus on number and distributions of trees of different size classes that should be left during harvest. This approach is consistent with our discovery that focus on nest trees is probably more important that broader habitat requirements. Some forest plans do argue that foresters should create a clumped distribution by leaving reserve trees in hollows or along stand borders or by retaining active nest trees and a clump of surrounding trees (Table 4). Considering our results, the focus on clumped distribution also seems appropriate.

5. Conclusion

This study indicates that vegetation surrounding nest trees may have minimal influence on woodpecker nest tree selection. Traditional emphasis on nest tree characteristics may be more appropriate. However, research that confirms this finding is needed. Research should be done that compares woodpecker use of nest trees before and after logging of adjacent vegetation. If researchers can document that woodpeckers continue to use nest trees after surrounding vegetation is altered, forest managers can be more confident that a focus on providing suitable nest trees is appropriate.

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References

Adkins Giese, C.L., 1999. Woodpecker nest site selection in oak forests of the Driftless Area in the Upper Midwest. M.S. Thesis. University of Minnesota, St. Paul, MN.

Adkins Giese, C.L., 2002. Woodpecker nest tree characteristics in Upper Midwestern oak forests. Wilson Bull., submitted for publication.

Box, G.E., Cox, D.R., 1964. An analysis of transformations. J. R. Statist. Soc. B 26, 211–243.

Brawn, J.D., Tannenbaum, B., Evans, K.E., 1984. Nest site characteristics of cavity nesting birds in Central Missouri. USDA Forest Service Research Note No. NC-314.

Bull, E.L., Meslow, E.C., 1977. Habitat requirements of the pileated woodpecker in northwestern Oregon. J. For. 75, 335–337.

Conner, R.N., 1978. Snag management for cavity nesting birds. USDA Forest Service General Technical Report No. SE-14, pp. 120–128.

Conner, R.N., Adkisson, C.S., 1977. Principal components analysis of woodpecker nesting habitat. Wilson Bull. 89, 122–129.

Conner, R.N., Hooper, R.G., Crawford, H.S., Mosby, H.S., 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39, 144–150.

Conner, R.N., Miller Jr., O.K., Adkisson, C.S., 1976. Woodpecker dependence on trees infected by fungal heart rots. Wilson Bull. 88, 575–581.

Dickson, J.G., Conner, R.N., 1983. Snag retention increases bird use of clearcut. J. Wildl. Manage. 47, 799–804.

Evans, K.E., Conner, R.N., 1979. Snag management. In: DeGraaf, R.M., Evans, K.E. (Eds.), Management of North Central and Northeast Forests for Nongame Birds. USDA Forest Service General Technical Report No. NC-51, pp. 214–225.

Gibbons, P., 1994. Sustaining key old-growth characteristics in native forests used for wood production: retention of trees with hollows. In: Norton, T.W., Dovers, S.R. (Eds.), Ecology and Sustainability of Southern Temperate Ecosystems, pp. 59–84.

Green, J.C., 1995. Birds and Forests: A Management and Conservation Guide. Minnesota Department of Natural Resources, St. Paul, MN.

Harrison, H.H., 1975. A Field Guide to the Birds' Nests East of the Mississippi River. Houghton Mifflin Company, New York, NY.

Howe, R.W., Niemi, G., Probst, J.R., 1995. Management of western Great Lakes forests for the conservation of neotropical migratory birds. USDA Forest Service General Technical Report No. NC-187, pp. 144–167.

Jackman, S.M., 1974. Woodpeckers of the Pacific Northwest: their characteristics and their role in the forests. Thesis. Oregon State University, Corvallis, OR.

Johnson, J.W., Wichern, D.W., 1992. Applied Multivariate Statistical Analysis, 3rd ed. Prentice-Hall, Upper Saddle River, NJ.

Keisker, D.G., 1987. Nest tree selection by primary cavity nesting birds in south-central British Columbia. Wildlife Report No. R-13. Wildlife Brach, Ministry of Environment and Parks, Victoria, BC.

Kilham, L., 1971. Reproductive behavior of yellow-bellied sapsuckers. I. Preferences for nesting in *Fomes*-infected aspens and nest hole interrelations with flying squirrels, raccoons, and other animals. Wilson Bull. 83, 159–171.

Kuehl, R.O., 1994. Statistical Principles of Research Design and Analysis. Duxbury Press, Belmont, CA.

Land, D., Marion, W.R., O'Meara, T.E., 1989. Snag availability and cavity nesting birds in slash pine plantations. J. Wildl. Manage. 53, 1165–1171.

Lawrence, L.D., 1966. A comparative life-history study of four species of woodpeckers. Ornithology Monographs No. 5.

Li, P., Martin, T.E., 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108, 405–418.

Mannan, W.R., Meslow, E.C., Wright, H.M., 1980. Use of snags by birds in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44, 787–797.

Marschner, F.J., 1974. The original vegetation of Minnesota (map). USDA Forest Service North Central Forest Experiment Station, St. Paul, MN (redraft of the original 1930 edition).

Martin, T.E., Conway, C.J., 1994. Breeding Biology Research Database (BBIRD) Field Protocol. Montana Cooperative Fish and Wildlife Research Unit, Missoula, MT.

McClelland, B.R., 1977. Relationships between hole-nesting birds, forest snags, and decay in western larch-Douglas fir forests in the northern Rocky mountains. Ph.D. Thesis. University of Montana, Missoula, MT.

McClelland, B.R., Frissell, S.S., 1975. Identifying forest snags useful for hole-nesting birds. J. For. 73, 414–417.

Niemi, G.J., Hanoski, J.M., 1984. Relationships of breeding birds to habitat characteristics in logged areas. J. Wildl. Manage. 48, 438–443.

Oehlert, G.W., Bingham, C., 1998. Macanova: Interactive Program for Statistical Analysis and Matrix Algebra, St. Paul, MN.

Petit, D.R., Grubb Jr., T.C., Reichardt, L.J., 1985. Habitat and snag selection by woodpeckers in a clear-cut: an analysis using artificial snags. Wilson Bull. 97, 525–534.

Raphael, M.G., White, M., 1984. Use of snags by cavity nesting birds in the Sierra Nevada. Wildlife Monographs No. 86.

Reller, A.W., 1972. Aspects of behavioral ecology of the red-headed and red-bellied woodpeckers. Am. Midl. Nat. 88, 270–290.

Robbins, C.S., Bruun, B., Zim, H.S., 1983. A Guide to Field Identification: Birds of North America. Golden Press, New York, NY.

Runde, D.E., Capen, D.E., 1987. Characteristics of northern hardwood trees used by cavity nesting birds. J. Wildl. Manage. 51, 217–223.

Ryan, T.M., 1995. Snag use by breeding birds in northern Wisconsin clearcuts. M.S. Thesis. University of Wisconsin, Stevens Point, WI.

Schulte, L.A., Niemi, G.J., 1998. Bird communities of early successional burned and logged forest. J. Wildl. Manage. 62, 1418–1429.

Scott, V.E., 1978. Characteristics of ponderosa pine snags used by cavity nesting birds in Arizona. J. For. 76, 26–28.

Scott, V.E., Oldemeyer, J.L., 1983. Cavity-nesting bird requirements and response to snag cutting in ponderosa pine. In: Davis, J.W., Goodwin, G.A., Ockenfels, R.A. (Tech. coords.), Proceedings of the Symposium on Snag Habitat Management. USDA Forest Service General Technical Report No. RM-99.

Scott, V.E., Evans, K.E., Patton, D.R., Stone, C.P., 1977. Cavity-nesting Birds of North American Forests. USDA Forest Service Agricultural Handbook No. 511.

Scott, V.E., Whelan, J.A., Svoboda, P.L., 1980. Cavity nesting birds and forest management. In: Management of Western Forests and Grasslands for Nongame Birds. USDA Forest Service General Technical Report No. INT-6, pp. 311–324.

Sedgwick, J.A., Knopf, F.L., 1986. Cavity nesting birds and the cavity tree resource in plains cottonwood bottomlands. J. Wildl. Manage. 50, 247–252.

Sedgwick, J.A., Knopf, F.L., 1990. Habitat relationships and nest site characteristics of cavity nesting birds in cottonwood floodplains. J. Wildl. Manage. 54, 112–124.

Shreiber, B., deCalesta, D.S., 1992. The relationship between cavity nesting birds and snags on clearcuts in western Oregon. For. Ecol. Manage. 50, 299–316.

Stauffer, D.F., Best, L.B., 1982. Nest-site selection by cavity nesting birds of riparian habitats in Iowa. Wilson Bull. 94, 329–337.

Stribling, H.L., Smith, H.R., Yahner, R.H., 1990. Bird community response to timber stand improvement and snag retention. Nor. J. Appl. For. 7, 35–38.

Styskel, E.W., 1983. Problems in snag management implementation—a case study. In: Davis, J.W., Goodwin, G.A., Ockenfels, R.A. (Tech. coords.), Proceedings of the Symposium on Snag Habitat Management. USDA Forest Service General Technical Report No. RM-99, pp. 24–27.

Swallow, S.K., Gutierrez, R.J., Howard, R.A., 1986. Primary cavity-site selection by birds. J. Wildl. Manage. 50, 576–583.

Thomas, J.W., Anderson, R.G., Maser, C., Bull, E.L., 1979. Snags. In: Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. USDA Forest Service Agricultural Handbook No. 553, pp. 60–77.

US Forest Service, 1981. Land and resource management plan: Eastern Region. USDA Forest Service, Eastern Region.

US Forest Service, 1986a. Land and resource management plan: Mark Twain National Forest. USDA Forest Service, Eastern Region.

US Forest Service, 1986b. Land and resource management plan: Shawnee National Forest. USDA Forest Service, Eastern Region.

US Forest Service, 1987a. Land and resource management plan: Hoosier National Forest. USDA Forest Service, Eastern Region.

US Forest Service, 1987b. Land and resource management plan: Wayne National Forest. USDA Forest Service, Eastern Region.

US Forest Service, 1988. Land and resource management plan: Allegheny National Forest. USDA Forest Service, Eastern Region.

US Forest Service, 1995. Land and resource management plan: Monogahela National Forest. USDA Forest Service, Eastern Region.

Welsch, C.J., Howard Jr., R.A., 1983. Characteristics of snags influencing their selection by cavity nesting birds. Trans. Northeast Fish Wildl. Conf. 40, 177.

Westworth, D.A., Telfer, E.S., 1993. Summer and winter bird populations associated with five age-classes of aspen forest in Alberta. Can. J. For. Res. 23, 1830–1836.

Winternitz, B.L., Cahn, H., 1983. Nest holes in live and dead aspen. In: Davis, J.W., Goodwin, G.A., Ockenfels, R.A. (Tech. Coords.), Proceedings of the Symposium on Snag Habitat Management. USDA Forest Service General Technical Report No. RM-99, pp. 102–107.

Zarnowitz, J.E., 1983. The effect of forest management on cavity nesting bird populations in the Olympic National Forest, Washington. For. Abstr. 44, 702.

Zarnowitz, J.E., Manuwal, D.A., 1985. The effects of forest management on cavity nesting birds in northwestern Washington. J. Wildl. Manage. 49, 255–263.